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Interference from adults forces young red knots to forage for longer and in dangerous places

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In birds and mammals, juvenile and adult foragers are often found apart from each other. In this study, we found this is also true for red knots, *Calidris canutus canutus*, wintering on the intertidal flats of Banc d'Arguin, Mauritania. Not only did juveniles feed separately from adults, they also fed at places where they were more vulnerable to predation by large falcons. That the dangerous areas used by juveniles were no better feeding areas led us to reject the food–safety trade-off that explained age-related distribution differences in many earlier studies. Instead, juveniles were displaced by adults in dyadic interactions which suggests that they suffered from interference from adults. Juveniles retreated to feeding areas that were more dangerous and yielded lower intake rates, and coped by extending foraging time by using higher, nearshore intertidal areas that were exposed for longer. When disturbed by predators in these nearshore areas, juveniles continued feeding whereas adults left. Thus, rather than compensating for increased predation danger by higher intake rates, on the Banc d'Arguin red knot juveniles foraged for longer.

Foraging animals must choose between locations that differ in many aspects, but food conditions and safety usually explain a lot of the variation found (van Gils, Edelaar, Escudero, & Piersma, 2004; Piersma, 2012). It is theoretically plausible (Houston & McNamara, 1999; Houston, McNamara, & Hutchinson, 1993) and has been empirically demonstrated (reviews by Brown, 1999; Brown & Kotler, 2007; Cresswell, 2008; Lima, 1998) that individuals are capable of responding in adaptive ways to trade-offs between energy gain and safety from predators, trade-offs that may be mediated by the energy state of the animal (Barnett, Bateson, & Rowe, 2007; Kotler, Brown, Mukherjee, Berger-Tal, & Bouskila, 2010; Real & Caraco, 1986). According to the ideal free distribution model, foragers should aggregate at patches where their food is most abundant. If patches also differ in safety, prey tend to aggregate in safer patches, even when these patches are relatively poor in resources (Heithaus, 2001; Hugie & Dill, 1994). Ultimately, owing to the balanced effects of interference, safety in numbers and habitat choice by their own predators, foragers are generally considered to trade rich and dangerous feeding opportunities against poor and safe options (Bednekoff, 2007; Hugie & Dill, 1994; Moody, Houston, & McNamara, 1996).

However, individuals differ in their position on the food–safety continuum (Houston & McNamara, 1999; Stephens & Krebs, 1986). For instance, foraging animals that balance energy intake and expenditure are expected to choose to forage in areas that are safest from predators even when these areas are less rewarding (Brown, 1988; van Gils et al., 2004; Houston & McNamara, 1999). Other individuals may forage in more danger-prone ways, for instance because hunger forces them to exploit the rewards of dangerous areas (see studies reviewed in Lima & Dill, 1990), or because inferior competitive abilities and inexperience prevent them from satisfying their daily requirements in the presence of dominants (Cresswell, 1994; Parker & Sutherland, 1986). Models of adaptive behaviour then predict that greater danger is compensated for by higher energy intake rates (Houston & McNamara, 1999). Indeed, this is corroborated by field observations in a wide range of species (reviewed in Lima & Dill, 1990). For example, in a Scottish estuary in winter, adult and juvenile redshanks, *Tringa totanus*, segregated into two areas, a mussel bed and a saltmarsh (Cresswell, 1994). Juveniles were excluded from the mussel bed by adults. Predation danger at the saltmarsh was much higher than at the mussel bed, but food abundance was higher as well so that juvenile redshanks in the saltmarsh achieved the highest intake rates.

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The present study at Banc d'Arguin, Mauritania, can in the first place be regarded as a verification of the age-related differences in foraging distributions shown by Cresswell (1994), albeit in a tropical setting and for a different shorebird species, the red knot, *Calidris canutus canutus*. It can also be regarded as another test of the general idea that predation danger and intake rates may be traded off in class-specific distributional decisions. We investigated age-related foraging patterns in the context of food and predator abundance and tested whether the previous finding that juveniles accept danger in return for better food is more generally observed.

METHODS

Study System

Up to 256 000 red knots (over 75% of the flyway population of this subspecies; Piersma, 2007) have been estimated to winter at Banc d'Arguin (Davidson & Piersma, 2009; Hagemeijer et al., 2004). Adults arrive from late August onwards, followed by juveniles a month later (Davidson & Piersma, 2009). Most birds leave Banc d'Arguin in late April and early May to breed in north-central Siberia (Dick, Piersma, & Prokosch, 1987; Piersma et al., 1990), returning in August–September, but they generally do not go north before their third calendar year (Piersma, van Gils, & Wiersma, 1996).

We assumed that the red knots we studied in the nonbreeding season followed a satisficing strategy, that is, they balanced energy intake and expenditure, at least until they started preparing for migration to the breeding areas (van Gils, Battley, Piersma, & Drent, 2005). This means that they chose the safest foraging areas as long as these allowed them to balance gross energy intake rate and energy expenditure (Nonacs & Dill, 1993). At the Banc d'Arguin this would mean that they should avoid nearshore areas, where the presence of raptor-concealing cover makes them vulnerable to surprise attack by large falcons (Dekker & Ydenberg, 2004; van den Hout, Spaans, & Piersma, 2008; Rogers, Battley, Piersma, van Gils, & Rogers, 2006). Despite this prediction we observed that most red knots caught by falcons were in fact juvenile (van den Hout et al., 2008). In the present study, we were able to assess the roles of conspecific density and interference (Sutherland, 1996; Vahl, van der Meer, Weissing, van Dullemen, & Piersma, 2005) because before and immediately after high tide shorebirds are forced to forage together, a feature of tidal systems exploited before in studies of oystercatchers, *Haematopus ostralegus* (Ens & Goss-Custard, 1984; Goss-Custard & Durell, 1987; Sutherland & Koene, 1982; Zwarts, Ens, Goss-Custard, Hulscher, & Durell, 1996).

Following Lank and Ydenberg (2003), we define 'danger' and 'risk' as follows. 'Danger' depends on predator abundance and habitat structure and thus is essentially an attribute of the environment. 'Risk' is the probability of a bird being caught, which is a function of both danger and the antipredator measures taken by prey through behaviour (Caro, 2005; Cresswell, 2008; Lima & Dill, 1990) or body composition (van den Hout, Mathot, Maas, & Piersma, 2010; van den Hout, Piersma, Dekinga, Lubbe, & Visser, 2006; Lima, 1986).

Study Area

The Parc National du Banc d'Arguin is an area of shallow water, intertidal sand- and mudflats and islands along the northern Atlantic coast of Mauritania, bordering the Sahara desert from about 20°50′N, 16°45′W to 19°20′N, 16°28′W (Isenmann, 2006; Wolff, 2005; Wolff & Smit, 1990). It covers an area of 12 000 km^2, 500 km^2 of which is intertidal. Much of the Banc d'Arguin is covered by vast sea grass beds on the intertidal flats mainly consisting of *Zostera noltii* (Altenburg, Engelmoer, Mes, & Piersma, 1982; van Gils et al., 2012; Isenmann, 2006; Wolff & Smit, 1990).

We studied red knots on the Iwik Peninsula (19°53′N, 16°17′W) during the winters of 2002/2003 to 2008/2009, and in 2010/2011. The central part of the peninsula consists of low barren hills (not higher than 15 m), as well as the central part of site 7 (Fig. 1a), which were favoured resting and perching sites of large falcons (lanner, *Falco biarmicus*, barbary, *Falco pelegrinoides*, and peregrine falcon, *Falco peregrinus*), and also functioned as points of departure for their attack flights. Low dunes border the mudflats in areas 1 and 2 (Fig. 1a). These are used by large falcons as cover for surprise attacks on shorebirds. Some sea grass beds (sites 8 and 9; Fig. 1a) are separated from the peninsula by an approximately 1–1.5 km wide channel. Other sites, including 6, 7, 10 and 11 (Fig. 1a), are separated from the peninsula by narrow channels of 150–250 m.

Age Distribution

Observations with a telescope (20–60× magnification) allowed us to distinguish juveniles from adults by plumage. Juveniles were characterized by their whitish underparts with a pink-buff wash and greyish brown upperparts; the coverts had pale fringes and dark subterminal lines (Prater, Marchant, & Vuorinen, 1977). Although these characteristics gradually faded in the course of winter, some inner grey-brown coverts with subterminal bars remained. Even when these bars had been lost, the brownish coverts were distinctive.

We examined flock sizes and age compositions at low tide (from 3 h before until 3 h after low tide). We made sure that all habitat types in as large an area as possible were covered (Fig. 1). Birds and flocks were assigned to habitat type and site (see Fig. 1a); for 421 of the 696 flocks exact GPS positions were recorded (Fig. 1b). All field observations on flock sizes and age distribution were done by P.J.v.d.H. The overall contribution of juveniles to the local population was estimated by dividing the total number of juveniles observed across all areas by the total number of birds sampled. Owing to limited access to offshore sea grass beds in the early years, we were not able to establish separate year-to-year estimates and used an overall estimate of the juvenile percentage in the population.

Predation Danger

During 1239 h of observations divided over 320 sessions which lasted on average 4.0 h (range 0.5–12 h) a total of 26 different observers recorded the presence of predators. Predators included mainly falcons and harriers (mainly marsh harrier, *Circus aeruginosus*, and an occasional Montagu's harrier, *Circus pygargus*). Kestrels, *Falco tinnunculus*, although commonly encountered, were not considered to be dangerous to shorebirds, and were therefore not included in analyses. Several other raptor species (black kite, *Milvus migrans*, Bonelli's eagle, *Hieraaetus fasciatus*, and golden eagle, *Aquila chrysaetos*) were observed only once. Jackals, *Canis aureus*, were occasionally seen, but during daylight hours hardly seemed to disturb shorebirds. As hunting predators tended to move over much larger areas than foraging shorebirds, each predator observation was assigned to one of the subsites in which we divided up the study site (see Fig. 1; van den Hout et al., 2008).

Responses to Predation Danger

We measured responsiveness to predation danger through behaviour and body state. As raptors as a rule rely on opportunities to catch their prey during surprise attacks, habitat structures that conceal attacks, such as dunes, significantly contribute to predation danger by increasing the lethality of attack (Cresswell, Lind, &

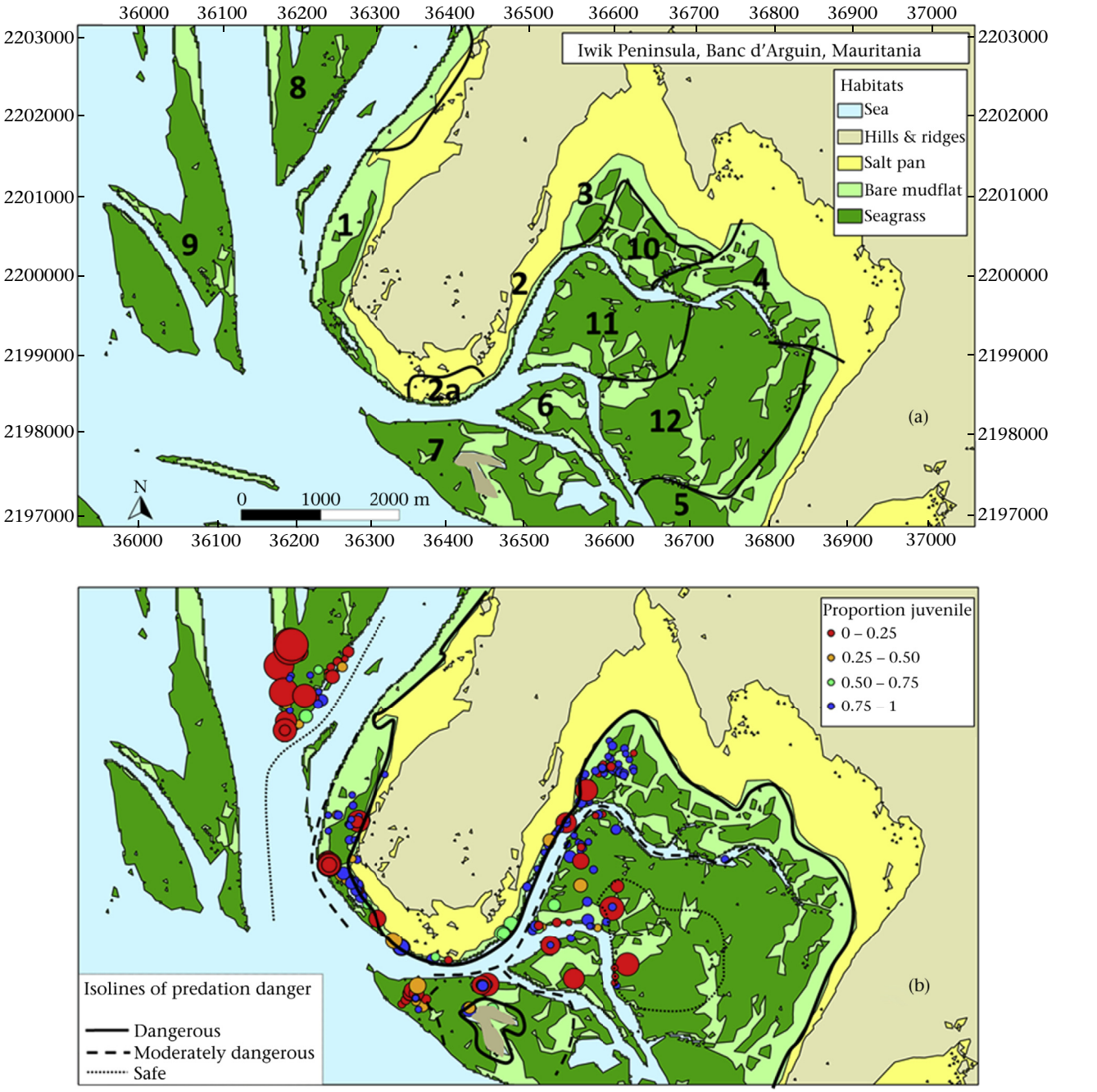

Figure 1. (a) Study area, showing subsites. Coordinates are in UTM. (b) Age composition (expressed as proportion of birds that is juvenile) for 421 flocks of red knots, between 3 h before and 3 h after low tide; exact positions were mapped. The size of the dots represents group sizes ranging from 1 to 600 (square-root transformed to decrease size range for ease of viewing). The isolines are the lines extending from places where raptors tended to start an attack (Iwik Peninsula, and subsite 7, where an observation tower provided a resting place for falcons) beyond which areas were found to be dangerous, moderately dangerous or safe with respect to predation.

Quinn, 2010). We recorded the proportion of time spent vigilant with respect to predator encounter frequency, distance from cover and flock size. Head-up vigilance was defined as the raising of the head from a head-down foraging position to at least a horizontal position (Metcalfe, 1984).

We assessed responses of foragers to the threat of attack while tallying age composition in flocks. Every now and then the flock under observation was disturbed by a raptor and took flight. If the age composition had been assessed just before the time of disturbance, it was possible to compare flock size and age composition before and immediately after disturbance.

Food Distribution and Intake Rates

We sampled benthic food availability in a stratified random fashion across our study area taking care to consider the two distinct intertidal areas: bare and sea grass covered (see Honkoop, Berghuis, Holthuijsen, Lavaleye, & Piersma, 2008). During April 2007, 448 samples were taken, evenly distributed over seven sampling stations throughout the study area (see van Gils et al., 2013 for details). In addition 56 samples were collected from sea grass habitat (20 in December 2003, 10 in December 2004, 20 in April 2005 and six in November 2006), and 85 samples from bare

habitat (50 in December 2003, 15 in December 2004 and 20 in April 2005). This involved taking a core (1/56 m^2) inserted in the sediment to a depth of 20 cm. To distinguish accessible from inaccessible prey (red knots have a bill length of 3–4 cm), the top layer (0–4 cm) was separated from the bottom layer (4–20 cm). Both layers were subsequently sieved over a 1 mm mesh. All prey remaining on the mesh were stored frozen for later analysis. Each prey was identified to species and size. Below we restrict our analyses to the fraction of bivalves available to red knots. Prey are considered to be available if they are both accessible (i.e. living in the top layer of the sediment) and ingestible (i.e. small enough to be swallowed whole; Zwarts & Wanink, 1993). With respect to the latter, maximal ingestible lengths were calculated based on a gape circumference limit of 30.6 mm for red knots (Zwarts & Blomert, 1992).

Red knots swallow shellfish whole, and process the items in their muscular gizzard (Piersma, Koolhaas, & Dekinga, 1993). Shell material is crushed and discarded through the intestine leaving the flesh to be digested. Therefore it is standard usage in analyses of bivalves as food for red knots (Dekinga & Piersma, 1993; van Gils, Battley, et al., 2005; van Gils, Piersma, Dekinga, & Dietz, 2003), to determine energy content and the amount of indigestible shell mass by separating the meat from the shell. We thus dried both flesh and shell to constant mass in a ventilated oven at 55–60 °C. The shell was then weighed to the nearest 0.001 g using an electronic balance. The dried flesh was incinerated at 550 °C for 2 h, after which we determined ash-free dry mass of the flesh ($AFDM_{flesh}$) by weighing it to the nearest 0.001 g on an electronic balance. For small bivalves and gastropods that did not allow separation of flesh and shell, dry mass and ash-free dry mass were determined from entire specimens; species-specific correction factors were used accounting for organic matter residing in the hard parts (van Gils, Spaans, Dekinga, & Piersma, 2006), and the loss of carbon in the incineration process. Prey quality, a major determinant of a knot's achievable daily intake rate under a digestive constraint (van Gils et al., 2003; van Gils, Dekinga, Spaans, Vahl, & Piersma, 2005; van Gils, de Rooij, et al., 2005), is the ratio between energy content of the prey ($AFDM_{flesh}$) and indigestible shell mass (DM_{shell}).

Energy intake rates were estimated by direct observation of swallowed prey items using a 20–60× zoom spotting telescope. Bird droppings were used to verify species composition, sizes and mass values of ingested prey items. At places where we had observed red knots foraging for at least half an hour, we collected samples of 50 droppings. Of the 76 samples, 25 were from bare habitat usually within 0–50 m off the shore and 51 from sea grass areas at various distances from the shoreline (28 samples from 50–250 m and 23 samples from 250–2000 m from shore). Droppings were stored frozen until analysis. Using a binocular microscope (Olympus SZ 51) we identified species and sorted them out to weight fractions. By using the species-specific relationships between hinge and umbo (the rounded apex of a bivalve) to length as derived from entire specimens, we could deduce the length classes of specimens in the diet of birds, their AFDM, the indigestible shell mass involved, and thus prey quality (Dekinga & Piersma, 1993; van Gils, Battley, et al., 2005; Onrust et al., 2013). We calculated instantaneous energy intake rates (mg $AFDM_{flesh}$/s), for adult and juvenile individuals, respectively, using the combination of item intake rates and average energy equivalents of the prey as deduced from the dropping analyses.

Prey composition in the field was estimated for three distance classes from shorelines (0–50 m, 50–250 m, 250–2000 m) by calculating species contributions expressed in $AFDM_{flesh}$. Likewise, to estimate diet composition, we derived prey compositions from droppings from juvenile-dominated (>50% juvenile) and adult-dominated (<50% juvenile) flocks.

Agonistic Interactions between Adult and Juvenile Foragers

To quantify the extent of competitive interactions between adults and juveniles, we studied flocks as they were crowding into nearshore habitat during the final stage of flooding between 10 and 25 October 2006. In area 1 (Fig. 1a) we conducted 103 group scans (Martin & Bateson, 1993), categorizing foraging habitat as either sea grass or bare sandflat. Scans of 5–10 min were made by slowly moving the telescope, at 20× magnification, from one side to the other, covering an angle of approximately 90°. Depending on the stage of the tide, the total area we scanned for birds varied between 50 and 400 m^2. We described each interaction in terms of age of the contestant (adult, juvenile or uncertain) and recorded the direction of aggressive displacements (adult displacing juvenile, or vice versa, and adults or juveniles displacing members of their own age group). Using the overall numbers of adults and juveniles present, we compared observed aggressive displacements between classes of individuals (adult–adult, juvenile–juvenile, adult–juvenile) with predictions under the assumption that age biases do not exist (Groves, 1978). For a mixed flock of adults and juveniles of any specified composition:

p = number of adults/(number of adults + number of juveniles)

q = number of juveniles/(number of adults + number of juveniles)

Thus, the expected frequencies of aggressive interactions, when interactions occur between random individuals, are p^2 and q^2 for aggression among adults and juveniles, respectively, and $2pq$ for adult over juvenile and juvenile over adult interactions. So, the relative probabilities of age-specific displacement events (P_{attack}) were assumed to depend on encounter probability between individuals ($P_{encounter}$) and the chance that, upon encounter, an aggressive displacement occurs ($P_{attack|encounter}$), such that:

$$P_{attack} = P_{encounter} \times P_{attack|encounter}$$

For all 92 group scans and each possible type of interaction the directions of deviations from expected frequencies were counted and evaluated by a chi-square test.

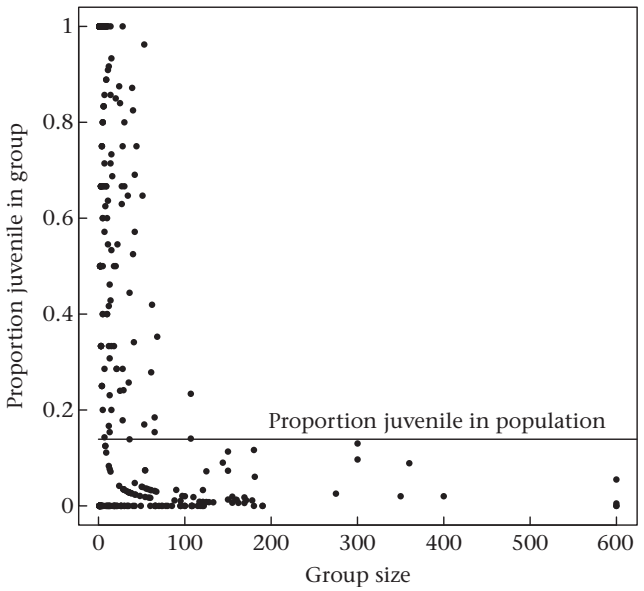

Figure 2. The proportion of juveniles as a function of flock size. The horizontal line shows the average proportion of juveniles in the population.

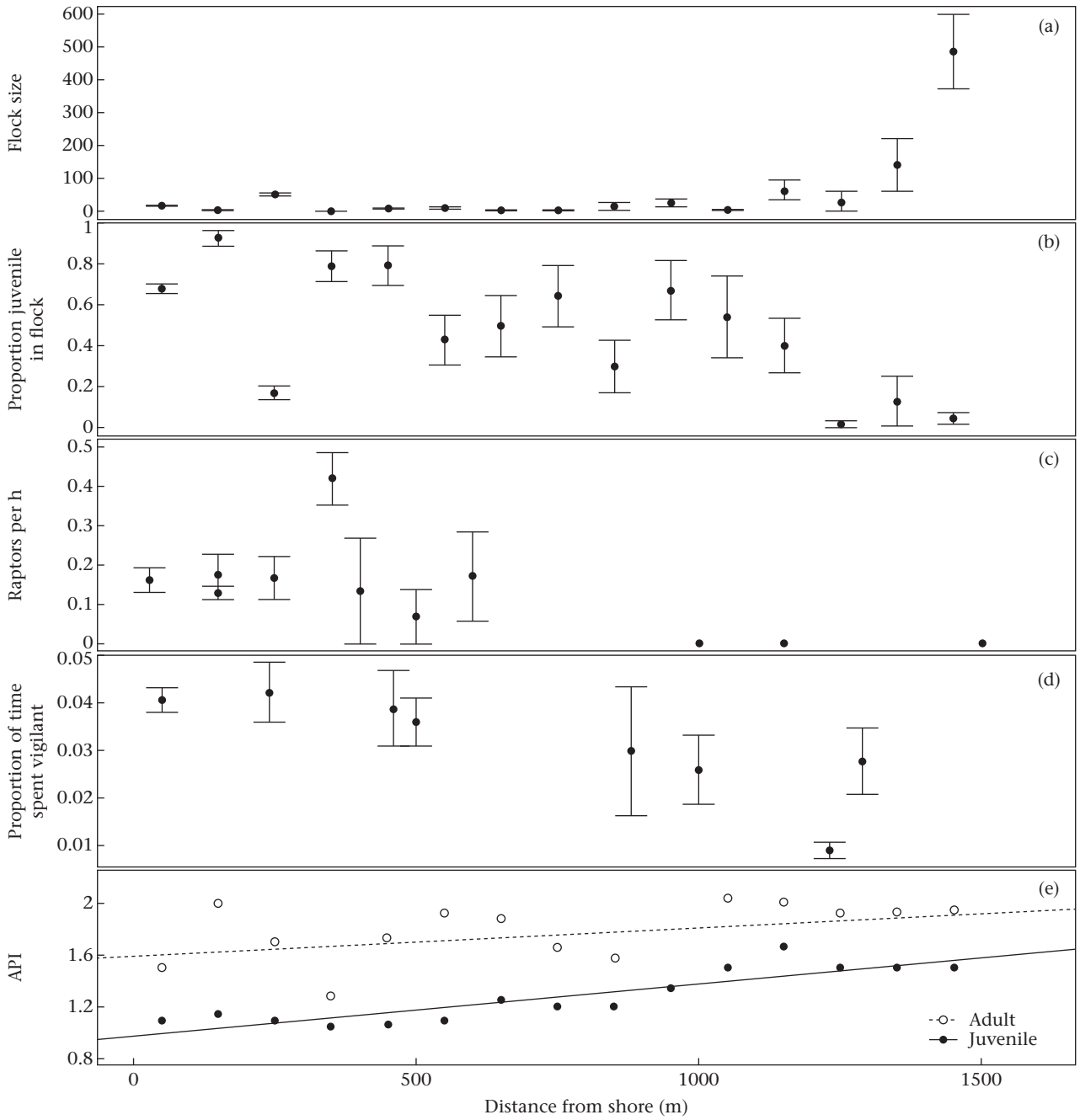

Figure 3. (a) Flock size of red knots as a function of distance from shore, at low tide (3 h before and after low tide). (b) The proportion of juveniles in a flock as a function of distance from shore. (c) Raptor encounter rate as a function of distance from shore. (d) Vigilance (measured as relative time devoted to vigilance) as a function of distance from shore. (e) Abdominal profile index (API) of adults and juveniles as a function of distance from shore.

Energy State and Gizzard Size

As demonstrated for waterfowl (van Gils et al., 2007; Madsen & Klaassen, 2006) and for red knots (van Gils et al., 2006; Wiersma & Piersma, 1995), estimates of body mass and fat load can be obtained by visual inspection of abdominal profiles. While recording site choice and flock size, we assessed abdominal profile indices (APIs) of adult and juvenile individuals in a range from 1 (very lean) to 5 (very fat) (Wiersma & Piersma, 1995) with a 20–60× zoom spotting telescope. To evaluate consistency of API recordings in the field, we tested for 14 birds whether variation in API corresponded to variation in body mass (Madsen & Klaassen, 2006), and found that it did (linear regression: $R^2_{\text{adjusted}} = 0.34$, $P = 0.04$; body masses were measured no more than 3 weeks before the API estimations).

Shell mass constrains the rate of energy intake (see above), while the level of this constraint is set by gizzard size (van Gils et al., 2003). To compare digestive capacities of age classes, gizzard sizes were measured in birds captured with mist nets at night (Leyrer et al., 2013; Leyrer, Spaans, Camara & Piersma 2006). This was done by A.D. during April 2007–2009 using an ultrasound apparatus with a 7.5 MHz linear probe (Pie 200, Pie Medical Benelux BV, Maastricht, The Netherlands; for further details, see Dietz, Dekinga, Piersma, & Verhulst, 1999).

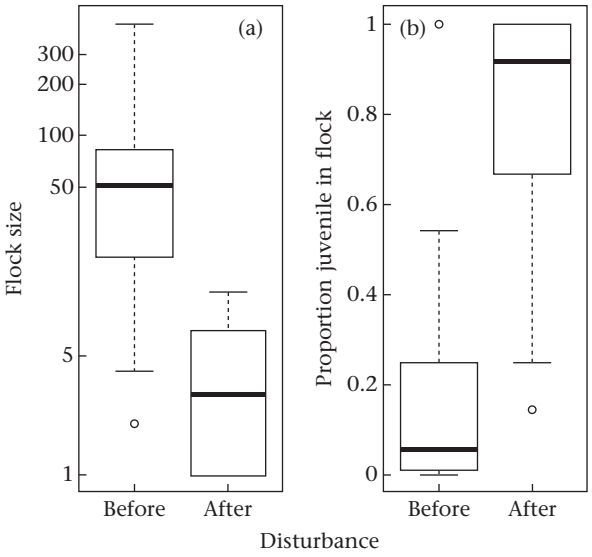

Figure 4. (a) Flock size (shown on a logarithmic scale) and (b) proportion of juveniles present in a flock before and after disturbance by a raptor (see text for further explanation). The horizontal line in each box plot shows the median value, the bottom and top of the box show the 25th and 75th percentiles (middle 50% of the data), respectively, while the whiskers show 1.5 times the interquartile range of the data. Points beyond these limits are plotted individually (open dots).

Statistics

All analyses were done in the R working environment (R Development Core Team 2012, version 2.15.1). We used logistic regression for binomial data on juvenile proportions (Warton & Hui, 2011). To deal with overdispersion caused by many zeros, for each binomial count we added a normally distributed random intercept term to the model (Warton & Hui, 2011) using the lme4 library in R (Bates, Maechler, & Bolker, 2012), or used a quasibinomial generalized linear model. A zero-inflated binomial model with log link from the library pscl (Jackman, 2012) was applied to test the number of raptors encountered as a function of distance to the shoreline. To examine whether the model fitted the data significantly better than the null model (the intercept-only model), we compared a quasibinomial generalized linear model to a null model without predictors using a chi-square test on the difference of log likelihoods. A Voung test was then applied to investigate further whether a model was an improvement above a standard Poisson model (procedure adopted from UCLA Academic Technology Services, University of California). All significance tests were two tailed.

RESULTS

At low tide, foraging juveniles and adults showed a clear segregation across spatial scales of hundreds to tens of metres (juveniles foraging in the vicinity of adult flocks, without mixing in; Fig. 1b). Across most flock sizes the percentage of juveniles in flocks deviated from the population mean of 14% (Fig. 2). Juveniles were underrepresented in flocks larger than approximately 60 birds and overrepresented in smaller flocks (generalized linear mixed model fitted by Laplace approximation: model: y ~ flock size + (1|occasion_id), z = −22,25, $df = 1$, $P < 0.001$). Closer to shore, flocks were smaller and consisted of relatively more juveniles (Fig. 3a, b; generalized linear model: $t = -3.2$, $P < 0.001$).

The probability of encountering a raptor declined with increasing distance from shorelines (Fig. 3c; zero-inflated binomial model with logit link: $z = -6.396$, $P < 0.001$). The proportion of time spent vigilant interacted with raptor encounter probability and increased with the proximity to shoreline (Fig. 3d; GLM logistic regression, quasibinomial: $t = -4.075$, $P < 0.001$). When disturbed by an aerial predator, flock sizes decreased from a mean ± SE of 74 ± 20 birds ($N = 25$) to a mean ± SE of 4 ± 1 individuals (Fig. 4a). The birds remaining after a raptor disturbance were largely juvenile (Fig. 4b; GLM, quasibinomial: $t = 4.743$, $P < 0.001$). When foragers were driven together at incoming tide (our 'semiexperiment'), juveniles suffered more aggression (both from adults and from other juveniles) than adults, both in sea grass and in bare habitat (Table 1; sea grass: $\chi^2 = 55.9$, $P < 0.001$; bare: $\chi^2 = 33.5$, $P < 0.001$). Red knots that foraged further offshore had higher API than those closer to shorelines (Fig. 3e; GLM: $t = 3.996$, $P < 0.001$), and although this relationship did not differ between adults and juveniles, adult APIs were generally larger than those of juveniles (Fig. 3e; GLM: $t = -7.153$, $P < 0.001$).

At 50–250 m from shore, food abundance was significantly higher than at both 0–50 m and 250–2000 m, with the latter two not being different (Fig. 5a; ANOVA: $F_{2,460} = 7.387$, $P < 0.001$; mean ± SE AFDM g/m^2 at 0–50 m = 2.47 ± 0.41; at 50–250 m = 3.41 ± 0.37; at 250–2000 m = 1.91 ± 0.09). Juveniles had lower instantaneous intake rates than adults, not only at the level of food items taken (mean ± SE = 2.38 ± 0.16 items/min versus 3.36 ± 0.21 item/min for adults), but also in terms of energy intake (mean ± SE = 0.18 ± 0.01 mg versus 0.39 ± 0.03 mg AFDM/s for adults). For both age classes, energy intake rates increased with distance away from shore, the factors 'age', 'distance class from shore' and their interaction all being significant (Table 2, Fig. 5b).

As shown previously (Honkoop et al., 2008), *Loripes lucinalis* was the most abundant species in sea grass areas, whereas *Dosinia isocardia* dominated in bare shoreline areas (Fig. 6a). *Dosinia* rather than *Loripes* prevailed in the diets of both adults and juveniles (Fig. 6b; consistent with recent findings by van Gils et al., 2013). Juvenile knots tended to feed more on *Dosinia* than adults across all sites (Fig. 6b). Juveniles in shoreline habitat fed nearly entirely on *Dosinia*, whereas their diet was much more varied offshore (Fig. 6c). Juveniles, but not adults, also included mud crabs, *Panopeus africanus*, in their diet (Fig. 6b, c). It is through this high-quality prey that juveniles in offshore areas of 250–2000 m experienced on average a higher food quality than adults, whereas the reverse was true for areas of 0–250 m from shore (Fig. 5c). This yields a significant interaction between age and distance from shore (Fig. 5c; ANOVA: $F_{2,259} = 24.66$, $P < 0.001$). Food quality in both adult and juvenile diets was lowest in nearshore areas (0–50 m from shore; Fig. 5c). Although with an average fresh weight of 9.28 g, gizzards of

Table 1
Summary of results from group scans recording age-related aggressive displacements between individual red knots at incoming tide

Habitat	N_{obs}	N_{ind}	% Juvenile	Relative probability of aggressive displacement (%)			
				Adult↔adult	Adult→juvenile	Juvenile→adult	Juvenile↔juvenile
Sea grass	56	1969	39	18.5	27.5	4.7	49.3
Bare	47	1377	35	31.2	18.0	3.9	47.0

The direction of the displacement (adult or juvenile chasing individual of their own age group, adult chasing juvenile and vice versa) is shown for various locations along the shoreline, grouped in sea grass and bare habitat.

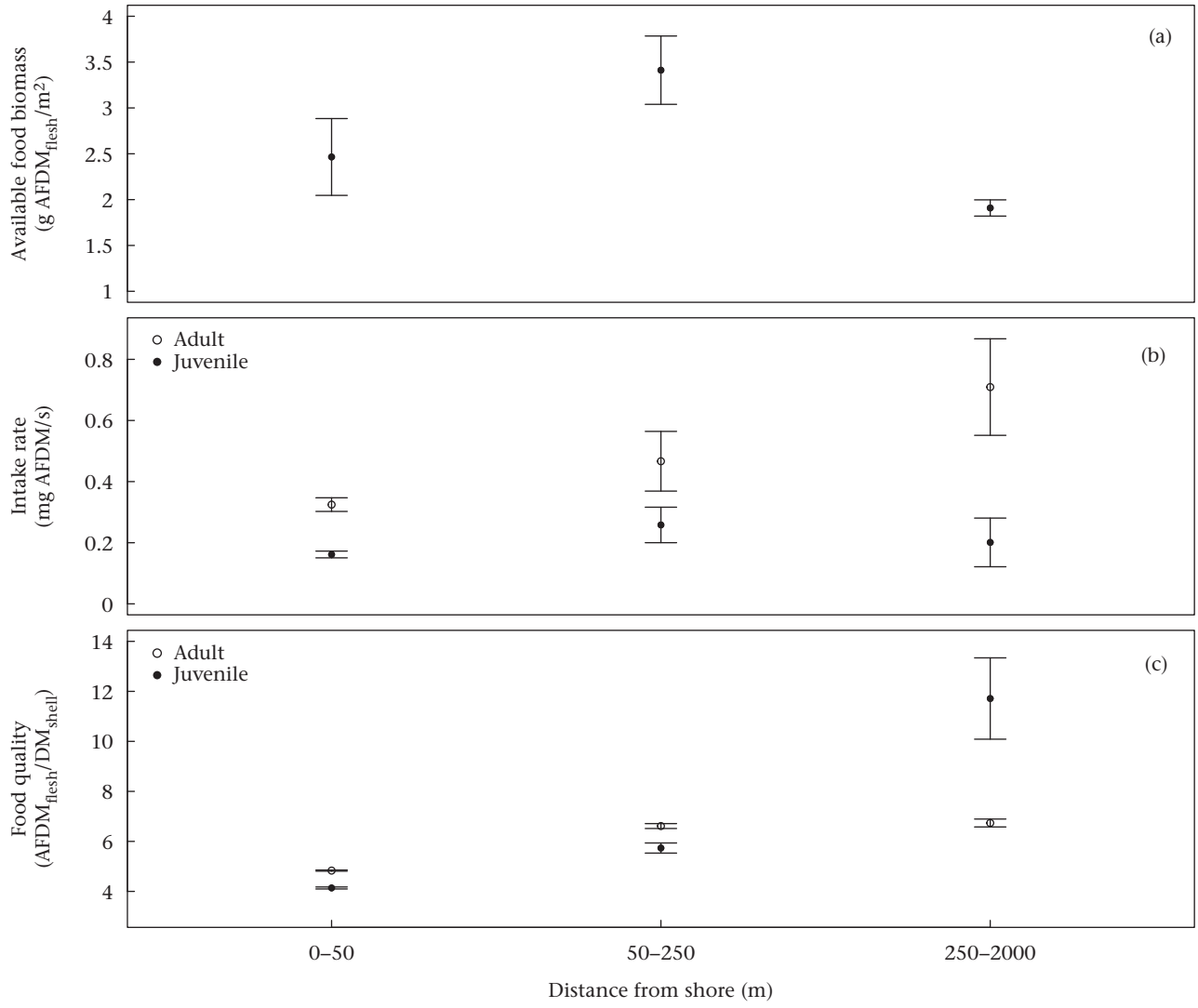

Figure 5. (a) Food availability (in ash-free dry mass of the flesh of prey, AFDM/m^2), (b) energy intake rates (mg AFDM/s) and (c) food quality as experienced by adults and juveniles, for three distance classes from shorelines (0–50, 50–250, 250–2000 m).

juveniles were smaller than those of adults at 10.0 g, the difference was not significant (Welsh two-sample t test: $t_{37.23} = -1.7732$, $P = 0.084$; $N_{adult} = 64$, $N_{juvenile} = 18$).

DISCUSSION

Around the Iwik Peninsula at Banc d'Arguin juvenile red knots foraged closer to shore where danger of predation by large falcons was higher. This closely resembles the description of redshanks foraging in a Scottish estuary (Cresswell, 1994). However, whereas juvenile redshanks attempted to forage with adults (and were chased off), juvenile red knots apparently avoided foraging in the presence of adults altogether, unless adults were forced upon them during the final stage of the incoming tide. As we have shown, this is probably because of their vulnerability to interference from adults, which means they would not achieve sufficient intake rates in their presence. Although their avoidance behaviour renders them at greater predation danger, unlike Cresswell's redshanks the juvenile red knots did not compensate for the danger with higher intake rates. In fact, intake rates in dangerous areas were lower than in safer areas. Therefore we firmly reject the food–safety trade-off hypothesis in the present case.

Our results suggest that juveniles, at sites that are more dangerous and yield lower intake rates, cope by foraging for longer. They achieved this extra feeding time by using nearshore areas, which remained exposed for longer (Fig. 7). This would nicely explain why foragers that need to spend at least 13 h foraging kept feeding in shoreline bare habitat zones during all stages of the tide (Fig. 7). That juveniles need to compensate for inferior competitive skills by foraging for longer is also indicated by the juveniles being far more reluctant than adults to interrupt their foraging activities when disturbed by an aerial predator. Even when nearby foragers collectively took flight upon disturbance, juveniles tended to stay put (Fig. 4). During such occasions we even observed adult flocks

Table 2
Analyses of variance of energy intake rates of red knots as a function of distance from shore

Independent variable	Sum of squares	*df*	*P*
Age	2.887	1	<0.001
Distance from shore (DFS)	1.014	2	<0.001
Age*DFS	0.632	2	0.004
Error	14.842	259	

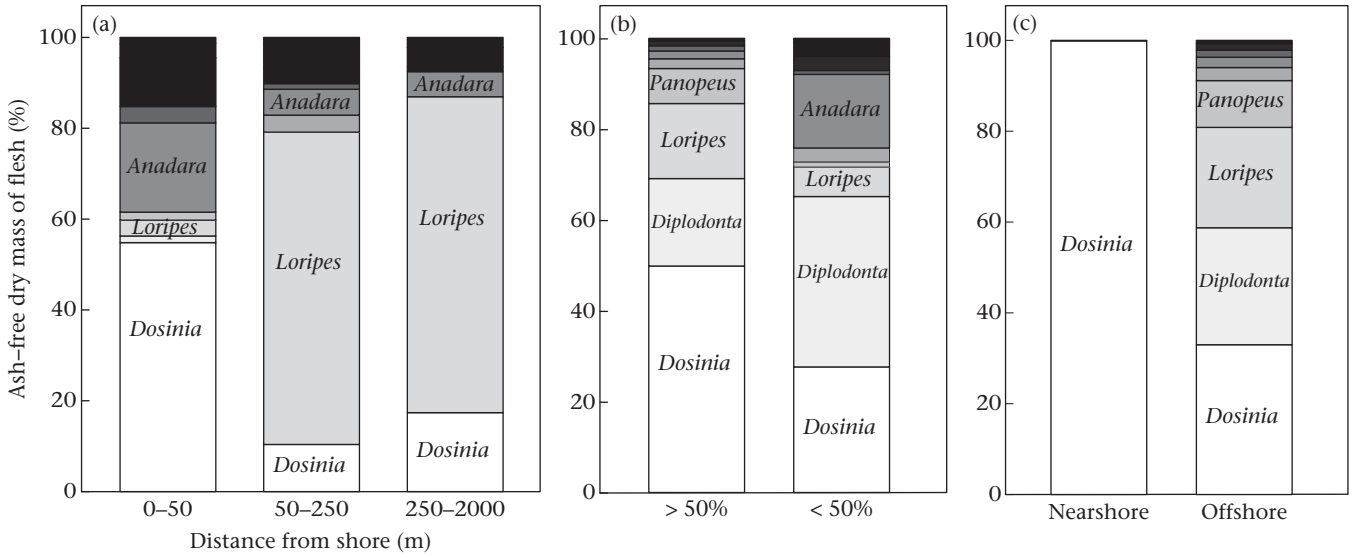

Figure 6. (a) Food composition in the field (expressed in ash-free dry mass of the flesh contained in prey) as derived from benthos sampling, for three distance classes from shorelines (0–50, 50–250, 250–2000 m). (b, c) Diet composition, as reconstructed from droppings, expressed in ash-free dry mass of the flesh contained in prey. (b) Flocks with more than 50% juveniles or less than 50% juveniles. (c) Juvenile-dominated flocks divided over nearshore bare areas (0–50 m from cover) and sea grass-covered areas further from shore. For ease of viewing, only the most important prey types are indicated, and species with an occurrence of less than 1% were pooled.

skimming low over foraging juveniles. The latter suggests that the observed age-related differences in escape decisions were not caused by differences in attentiveness (Ydenberg & Dill, 1986), but must have been caused by the fact that juveniles tolerate more danger as they are less willing to pay the costs of fleeing (cost of flight and loss of feeding opportunity).

Throughout the study area, and even when foraging away from adults, intake rates of juveniles were lower than those of adults. Although this is probably a consequence of juveniles being evicted from the best foraging areas, age differences in foraging skills may contribute to this difference. In general, juvenile shorebirds tend to be less efficient foragers than adults, and there is evidence that the greater the skill needed to find and handle prey, the less successful juveniles are compared to adults and the longer it takes them to acquire those skills (Durell, 2000; Durell, 2003; Wunderle, 1991). Red knot are foragers on buried bivalves in soft sediments that are located by a highly specialized technique of remote sensing (Piersma, van Aelst, Kurk, Berkhoudt, & Maas, 1998), and we have indications that the sea grass root systems interfered with the detection of these prey (J. de Fouw, unpublished data). That adults, and not juveniles, achieve highest intake rates in the 250–2000 m zone despite a lower food abundance (Fig. 5a, b) may be explained by lower vigilance costs due to their aggregated foraging in safe offshore areas. (Fig. 3d). It does not hold for the few juveniles here, which are apparently unable to benefit from flockmates for vigilance.

The observations around high tide suggest that juveniles are subordinate to adults and suffer direct forms of interference (Goss-Custard & Durell, 1987; Vahl, van der Meer, Meijer, Piersma, & Weissing, 2007). Although we did not study the mechanisms of interference in detail, we observed juveniles inspecting the successes of others more often than adults, thereby effectively eliciting agonistic interactions. The additional occurrence of cryptic interference (Bijleveld, Folmer, & Piersma, 2012) at low tide is suggested by the fact that even in places where juveniles did forage in the vicinity of adult-dominated flocks, rather than mixing in, they tended to forage on the periphery of these flocks. Bijleveld et al. (2012), in an indoor experiment, showed that foraging efficiency of subordinate red knots decreased in the presence of dominant competitors, even when interference was rare or absent.

The idea that the age-related distributions in the field emerge from differences in social status is consistent with the observations of Leyrer et al. (2012) in the same study area. At the larger spatial scale of roosting and adjacent foraging areas, Leyrer et al. observed a sex- and age-structured distribution of red knots. Since the larger females and the older birds predominated at the richest of the two areas, it was argued that differences in competitive ability

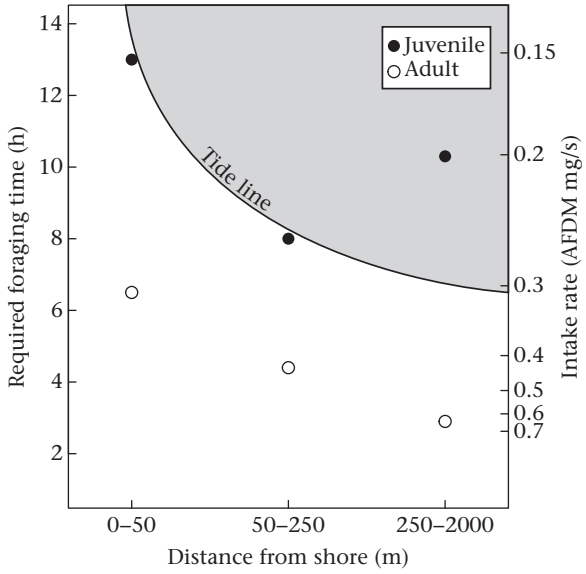

Figure 7. Minimal foraging time needed by foragers to gain required daily energy intake rate, dependent on their short-term intake rate, illustrating why poor foragers should feed closer to shorelines. Assuming a maintenance metabolism of 1.38 W at Banc d'Arguin (Piersma, 1994), we arrive at a minimal required daily energy of 119 kJ. With an energy density of 22 kJ/g $AFDM_{flesh}$ (Zwarts & Wanink, 1993), and an assimilation efficiency of 0.725 (Piersma, 1994), we can estimate the minimal time (excluding digestive breaks; van Gils, Dekinga, et al., 2005) that red knots need for foraging dependent on their energy intake rates. A smoothed tide line was added. Foragers that are in the grey surface area, owing to low intake rates (second y-axis), need more time than what is maximally available to cover their daily energy requirements.

maintained this spatial structure. The consistent phenotypic differences (in terms of API) across habitat zones (distances from shore) that we observed in our study (Fig. 3e), are also consistent with a structured distribution, and refute the idea that individuals regularly switch between offshore and nearshore areas. That nearshore foragers had lower API than the ones further from shore may be because these individuals respond to the higher predation danger by reducing body mass (mass-dependent predation risk; Carrascal & Polo, 1999; Gosler, Greenwood, & Perrins, 1995; Lima, 1986), just as we found in an indoor experiment with red knots (van den Hout et al., 2010). Yet, we cannot exclude the possibility that their low APIs reflect a hunger state caused by foraging constraints (e.g. van Gils et al., 2007).

Our results lead us to reject the idea of a food–safety trade-off (i.e. individuals feeding at dangerous places do so because of the higher energy rewards there). In contrast to Cresswell's juvenile redshanks (and the many other studies summarized in Lima & Dill, 1990), the juvenile red knots at Banc d'Arguin were not really able to compensate for danger with higher intake rates. By accepting higher levels of danger, however, the juveniles were able to compensate by foraging for longer at the high nearshore flats. They could do this without any disturbance from adult competitors (which satisfied their needs more quickly at the safer offshore areas, and thus could free up time for other activities). Our study shows that a sound understanding of bird distribution cannot be achieved on the basis of instantaneous distribution patterns alone, but must include how individuals adjust time budgets to prevailing foraging conditions.

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